



Seasonality, diaspore traits and the structure of plant-frugivore networks in Neotropical savanna forest



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ARTICLE INFO

Article history:

Received 1 December 2016

Received in revised form

4 July 2017

Accepted 8 August 2017

Available online 19 August 2017

Keywords:

Birds

Cerrado

Food resource

Lipid

Specialization

ABSTRACT

Complex frugivory networks are common in heterogeneous environments, but how the structure of those networks varies due to seasonality and other environmental factors remains unclear. For example, seasonal variation in rainfall can influence fruit production and diaspore characteristics, which could alter the quantity and quality of resources available to different animals in the network and, hence, network structure. We investigated how a frugivory network varied seasonally in Brazilian savanna (Cerrado), where there are well-defined dry and wet seasons and fructification mainly during the rainy season for most tree species. We recorded fruit consumption by animals during the dry and wet seasons in two different gallery forests and used these data to test the hypotheses that connectance, links per species and nestedness would be higher in the dry season than rainy season due to low available food in the former that would be consumed by various species of frugivores. Concomitantly, we also measured seed width and lipid content from diaspores of the fruiting trees to determine if these characteristics influenced interaction properties between fruiting trees and frugivores. Among the measured network parameters, connectance, links per species and specialization varied between seasons in one site but not in the other, indicating that seasonal variation in networks is not necessarily consistent over time or space. The number of tree species with small diaspores with high lipid content differed between seasons, and those characteristics were key factors increasing the interaction parameter of fruiting trees. We suggest that network stability between seasons may be related to local frugivore diversity, resource availability, and fruit quality.

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1. Introduction

The analysis of mutualistic networks is an important tool for understanding evolutionary processes and the maintenance of biodiversity (Bascompte and Jordano, 2007). The ecological interactions represented in these networks can be represented by graph structure, and quantified using metrics such as interaction strength, number of linked species and level of nested links (Cruz et al., 2013; Saavedra et al., 2014). In general, networks with many links between species, i.e., high connectance, are “nested”. This means that interactions mostly involve generalist species with

low resource specificity, generalist species with other generalists (i.e., “central core”), and generalist species with specialist species (Diaz-Castelazo et al., 2010).

Frugivory networks are a type of a mutualistic network characterized by low specificity (Carlo and Yang, 2011) and diverse interactions that are a typical response to environmental heterogeneity. Interactions between frugivores and fruiting tree species have been shown to be influenced by the extent of forest stratification (Schleuning et al., 2011), variation in landscape types (Cruz et al., 2013; Plein et al., 2013; Hawes and Peres, 2014), and human-induced edge effects (Saavedra et al., 2014). However, while seasonality may lead to variation in resources available to frugivores and, thereby, the strength and type of plant-frugivore interactions (Mulwa et al., 2013), how the structure of frugivory networks varies temporally remains surprisingly ambiguous

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(Gonzalez-Castro et al., 2012; Hawes and Peres, 2014).

The structure of consumer-resource networks has been shown to respond to temporal variation in resources at annual (Alarcón et al., 2008), daily (Fründ et al., 2011) or seasonal time scales (Winemiller, 1990; Akin and Winemiller, 2006; Berg and Bengtsson, 2007). The interactions, and hence network properties, may be dependent on the local-temporal context (i.e., food availability, abundance or richness of consumers) (Fründ et al., 2011; Perea et al., 2013; Poisot et al., 2015). In frugivory networks, a seasonal increase in food availability could cause an increase in the number of interactions (Carnicer et al., 2009; Plein et al., 2013; Ramos-Robles et al., 2016), thereby influencing seed dispersal (Gonzalez-Castro et al., 2012). Network structure can also vary temporally due to seasonal differences in the use of resources (Cruz et al., 2013; Santos et al., 2014) or seasonal patterns of rainfall (Takemoto et al., 2014) or presence of migratory frugivores (birds) (Ramos-Robles et al., 2016). Nevertheless, these results might not be universal. For example, connectance could also remain unchanged between seasons (Winemiller, 1990; Olesen et al., 2008) due to the fact that higher fruit abundance and long periods of fruiting might increase the probability of links between the species (Olesen et al., 2008).

Morphological and nutritional characteristics of fruits can influence fruit selection by frugivores (Howe, 2016). Smaller seeds (Hawes and Peres, 2014) and lipid-rich fruits (Schaefer et al., 2014) can be chosen rather than other characteristics. Both, size and fruit nutritional quality, can vary between seasons. Species that fruit in autumn in North America have larger seeds than species that produce fruit in other seasons (Piper, 1986), while those in temperate regions of Europe can have smaller seeds after the migratory season (Eriksson and Ehrlén, 1998). During the late autumn fruits can have high levels of protein (Johnson et al., 1985), while fruits can have high levels of lipids during the winter (Herrera, 1982). Moreover, the greatest fruit production occurs during the rainy season in the tropics (Levey, 1988), though it does vary seasonally with elevation (Loiselle and Blake, 1991). This seasonality apparently influences characteristics of networks (Gonzalez-Castro et al., 2012; Hawes and Peres, 2014) in ways that could potentially influence plant communities (Lange and Del-Claro, 2014).

Despite attempts to determine if networks predict ecological outcomes (Carlo and Yang, 2011), general conclusions regarding the influence of seasonality on the structure of frugivory networks remain elusive (Takemoto et al., 2014). In part this is because studies are based on presence or absence of interaction (i.e., 1, if Frugivore A consumes fruit of Plant 1; 0, if not; Schleuning et al., 2014) rather than number of interactions (Vizentin-Bugoni et al., 2016) or number of consumed fruits. Second, most studies to date have been conducted in the temperate zone, where the limited diversity of frugivores can limit the range of potential interactions (Carnicer et al., 2009; Plein et al., 2013), or have limited analyses to only a subset of potential dispersers (e.g. only birds) (Carnicer et al., 2009; Plein et al., 2013; Schleuning et al., 2014). Third, using techniques such as the analysis of fecal samples to assess frugivory rather than observations of focal plants (Carnicer et al., 2009) can preclude the collection of data such as the number of fruits eaten, number of seeds dropped, time spent in a tree, etc. Fourth, studies that have collected data throughout a full year are uncommon (Plein et al., 2013) but essential because longer sampling can give more accurate estimates of, for example, connectivity (Vazquez and Aizen, 2004) and modularity (Bosch et al., 2009). Finally, most studies rarely consider seasonality and diaspore characteristics simultaneously, despite the fact that species characteristics can be important to understand differences between specific interactions (microscopic level) that can be hidden by general interactions (macroscopic level) (Trøjelsgaard and Olesen, 2016).

Brazilian savannas, known broadly as Cerrado, are composed of

different phytophysionomies (Oliveira-Filho and Ratter, 2002), including gallery forests that border streams (Ribeiro and Walter, 2008) and that support a high diversity of zoochoric plants (Kuhlmann and Ribeiro, 2016). Marked seasonality in rainfall is typical of the region, which drives patterns of phenology and morphology – fruit production (Gouveia and Felfili, 1998) and seed size (Oliveira, 2008) are greatest during the rainy season. Here, we take advantage of the high plant and frugivore seasonality, and seasonal variability in fruit characteristics to investigate how seasonality influences frugivory network parameters. We hypothesize that during the dry season the reduced food availability will cause both generalist and specialist frugivores (consume sporadically and preferably fruits, respectively) to feed on available fruiting tree species (see Carnicer et al., 2009; Plein et al., 2013; Ramos-Robles et al., 2016). This will lead to more links between species and nested interactions in the dry season, and more specialized and modular interactions during the wet season. We then test the relationship between diaspore traits (morphology and nutritional content) and plant-frugivores interaction in each season (e.g. smaller seeds in dry season will permit interactions between tree A and diverse frugivores and will lead to high interaction strength).

2. Materials and methods

2.1. Study areas

We studied fruit-frugivore interactions in two gallery forests about 40 km apart in Federal District, Brazil (Fig. 1), where the dry season (average rainfall 800 mm) is from April–September and the wet season (average rainfall 2000 mm) is from October–March (Silva et al., 2008). The first gallery forest (GFA) borders two streams in the Águas Emendadas Ecological Station (ESEC-AE; 15°32'S 47°34'W, ~945 m a.s.l.), which is situated in the northwest portion of Federal District. ESEC-AE is a 10,547 ha protected area surrounded by highways and farms. The second gallery forest (GFB) borders two streams in the Água Limpa Experimental Farm (FAL, 15°57'S 47°56'W, ~1097 m a.s.l.), which is located in the southwestern portion of the Federal District. The area is a University of Brasilia property (4062 ha) and is adjacent to two other protected areas – the Brasilia Botanical Garden Ecological Station (5000 ha) and the Ecological Reserve of Brazilian Institute of Geography and Statistics (IBGE) (1360 ha).

Trees are the most diverse life form of zoochoric plants in Brazilian savanna gallery forest (Kuhlmann and Ribeiro, 2016). Inventories in these studied forests found high richness of zoochoric trees and frugivores. A survey of different gallery forests (0.48 ha total area surveyed) in ESEC-AE, including GFA, identified 78% of zoochoric individuals and 65% of zoochoric tree species (Haidar et al., 2013). A bird survey in ESEC-AE recorded 266 species (60.6% of the total recorded in Federal District), including 16 endemic to Brazilian savanna (Bagnó, 1998; Lopes et al., 2005). A survey totaling 1-ha in a section of GFB recorded 84% of zoochoric individuals and 74% of zoochoric tree species (Oliveira et al., 2011). Bird survey in FAL recorded 206 species (46.9% of the total known from Federal District) with 10 endemics species (Braz and Cavalcanti, 2001).

2.2. Data collection

We conducted focal observations at 10 zoochoric fruiting tree species at GFA from November 2013 to November 2014 (59 days – approx. 174 h – in dry season and 45 days – approx. 161 h – in wet season; observations by AABD) and at 12 tree species in GFB from March 1988 to January 1990 (50 days – approx. 180 h – in dry season and 46 days – approx. 165 h – in wet season; observations by

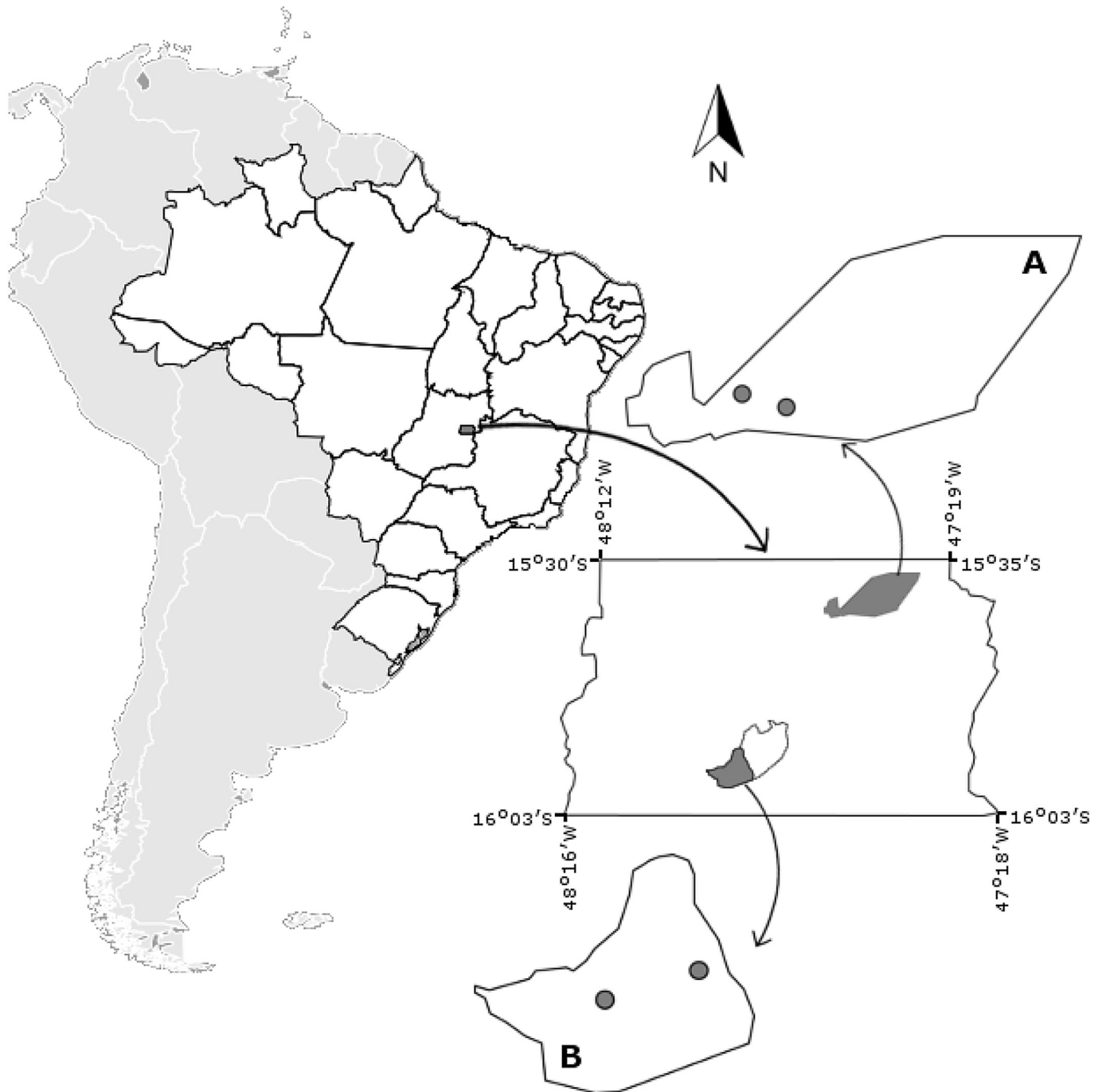


Fig. 1. Locations of gallery forest study sites in different protected areas about 40 km apart in the Federal District, Brazil. A: Águas Emendadas Ecological Station (ESEC-AE), where the first gallery forest is located (circles represent the sampling sites)- GFA; B: Água Limpa Experimental Farm (FAL), where the second gallery forest is located (circles represent the sampling sites)- GFB (white space at side represent other protected areas next to FAL).

JCM-J). Frugivores were recorded if they ate at least one fruit. Observations started in early morning (about 700 h) and finished late afternoon (1800 h). Most individual trees were observed for a total of 32 h at GFB and 36 h at GFA, although three species in GFA were observed for 18, 24 and 26 h and two species in GFB for from 10 to 15 h (Appendix Table A1). This number of hours is considered sufficient to document stable plant-animal interaction patterns (Vizentin-Bugoni et al., 2016). In both forests, we located trees for focal observations by walking trails in the study areas and looking for trees with ripe fruits or seeds with arils. Focal trees were located

in flooded and unflooded patches of forest, both inside and at the edge of the gallery forests. Most fruiting tree species were represented by three (GFA) or up to six individuals (GFB). Individuals were chosen for observations based on the amount of fruits and good canopy visibility. We collected voucher specimens from all focal trees and identified species by comparison with plants in University of Brasilia (UB) (GFA and GFB) and University of Campinas (UEC) (GFB) herbaria. Nomenclature for trees and frugivores follow Brazilian flora (<http://floradobrasil.jbrj.gov.br/>), checked by 'flora' package (version 0.2.7, <https://cran.r-project.org/web/>

packages/flora/index.html) in software R (version 3.1.2, <http://www.R-project.org>), and Brazilian Ornithological Records Committee (CBRO, 2014) or Annotated Checklist of Brazilian Mammals (Paglia et al., 2012), respectively.

We used 10 × 50 mm (Bushnell®) (GFA) and 8 × 30 mm (Carl Zeiss®) (GFB) binoculars to make observations; observations were recorded on field spreadsheets (GFA) or with voice recorders (GFB). Frugivores (birds and mammals) were identified based on morphology and vocalizations (only birds), using field guides (e.g. Meyer de Schauensee, 1970; Dunning, 1982; Gwynne et al., 2010) and the University of São Paulo and University of Brasília zoological museum collections. We recorded the identity of frugivores and the number of fruits eaten during a visit. After a frugivore left a fruiting tree, new foraging records for that species were recorded only after 5 min had passed, if there was only one individual of that species in the tree. If the species was represented by more than one individual in the tree, the 5-min rule was ignored and each individual was treated as a separate observation. Data were collected after the observer was in the place for 5 min at a distance of at least 15 m from the focal fruiting tree.

We collected a total of 100 (GFA by AABD) and 30 (GFB by JCM-J) fruits from three individuals of each focal tree species (about 30 and 10 fruits per tree) right before the period of observation has started. In other words, we collected for further analysis 500 (GFA) and 150 (GFB) fruits from tree species that have fruited in wet season and 500 (GFA) and 210 (GFB) fruits from tree species that have fruited in dry season. Fruits and seeds were measured (length, width) with metal callipers (0.1 mm) and weighed with a precision balance (0.0001 g). We only used seed width in subsequent analyses because morphological data from seed and fruit (e.g. mass; length; and width) were highly correlated (r^2 higher than 0.4 and $p < 0.01$). Pulp, including pericarp and aril, was removed from fruits and stored frozen for later chemical analyses. The total lipid content of fruits collected in GFA was determined by the gravimetric method (Melo et al., 2015). Triplicate samples previously dried on lyophilizer for 48 h were pulverized using a mortar and pestle. A sample of 50 mg was extracted with 2 mL of organic solvent hexane and placed in an ultrasound bath for 15 min. The supernatant was removed and a new extraction carried out twice more. The total solvent volume was evaporated at the chapel in a laminar flow hood for 48 h and the content of lipid estimated in a precision balance (0.0001 g). We could not measure the lipid content of *Xylopia emarginata* Mart. or *Guarea guidonia* (L.) Sleumer due the low amount of aril collected. These data were obtained from other studies (genus *Xylopia*, Christianini et al., 2012; *Guarea*, Lamperti et al., 2014). In general, there is no significant variation in this trait between species from the same genus (Jordano, 1995).

The lipid content of fruits collected in GFB was quantified according to standard methods (Folch et al., 1957). Homogenized ripe fruit from each species was used to obtain 200 mg of dry pulp or macerated aril. Only the employed organic solvent was modified in this method (distilled pure hexane instead of chloroform solution in methanol 1:2). The method used to lipid extraction was different for GFA and GFB because of the interval between the collection of fruits in each forest (about 20 years). Despite of both methods have used the gravimetry and organic solvent hexane to extract lipids, these methods has some differences, such as ultrasound in the former and filtration process in the latter. Moreover, each method was executed by a different person in different labs. Therefore, comparison between the results from these methods should be avoided and this comparison is not the aim of this study. We could not determine lipid content for *Alchornea glandulosa* Poepp. & Endl. or *Xylopia aromatica* (Lam.) Mart. and these data were obtained from other studies (*Alchornea glandulosa*, Pizo and Oliveira, 2001; genus *Xylopia*, Christianini et al., 2012).

2.3. Statistical analyses

Interaction matrices, with fruiting tree species as rows and frugivore species as columns, were used to construct a fruit-frugivore network for each season (dry and wet) and forest (GFA and GFB). The data used to fill these matrices were numbers of total fruits consumed by each animal species from each tree species. We followed Carlo and Yang (2011) and focused on five network parameters: (1) modularity (M, it represents the non-random interactions between groups of species that form, in this way, significant modules; ranges from 0 to 1); (2) nestedness (NODF, it measures how the observed pattern of interactions deviates from a perfectly nested pattern of interactions or, in other words, to what extent the observed links were not uniformly distributed among species; ranges from 0 to 100); (3) number of links per species (sum of links divided by number of species); (4) specialization (H_2 , it considers the deviation of observed interactions from interactions without apparent specialization of fruiting trees and animals - null distribution; ranges from 0 to 1); and (5) connectance (it is the proportion of observed in relation to all possible links between fruiting trees and animals, ranges from 0 to 1). We used NODF (nested overlap and decreasing fill) to measure this parameter as it is most consistent among the usual measures of nestedness (Almeida-Neto et al., 2008). H_2 is derived from the Shannon diversity index of network links (Blüthgen et al., 2006). We tested the significance of these parameters by using null models with 1000 replicates (type II) (Bascompte et al., 2003).

We used confidence intervals (CI) to compare parameters between seasons in each forest. Confidence intervals were obtained by running 1000 bootstrap iterations with replacement (Schleuning et al., 2011). We produced random databases with the same amount of observed records per month in each season. Then, randomly sampled matrices were formed and the network parameters were calculated. We used random values of each network parameter to obtain the CI by quantiles 95% (interval between 2.5% and 97.5%).

We fit generalized linear models (gamma distribution) with lipid content and seed width as explanatory variables and interaction properties of fruiting trees (species strength) as response variable to determine if coefficients for the explanatory variables were significantly different from zero. Species strength is the sum of interaction strength values of a fruiting tree with all animal species and interaction strength is the relative interaction between a fruiting tree and a particular animal (interaction value between fruiting tree and animal divided by total interactions of the animal). When the tree species had interactions in both networks (dry and wet), two species strength values were obtained. We then choose the species strength obtained from the network of season in which this tree species had a higher number of eaten fruits (higher sample effort). In this way, we were able to categorize in the analysis the effect of lipid content and seed width on plant-animal interactions in each season. The values of species strength (in GFA and GFB models), lipid (in GFA and GFB models) and seed width (only in GFB) were square-root transformed because of high variation in these values (Appendix Table A2).

The full generalized linear model of each forest included interaction terms between content of lipid and seed width plus interaction with seasons in order to evaluate the effect of seasonality. We tested the significance of this full model by comparison with a model without interaction between content of lipid and seed width (F test). We compared the ratio of the residual deviance to the residual degrees of freedom with the expected dispersion parameters to test if the models provide a good fit to the data.

All network analyses were run using the “bipartite” package (Dormann et al., 2009); other analyses were done using the “stats”

package in software R.

3. Results

The wet-season network in GFA included six tree species and 32 animal species (34% exclusive species); the dry-season network comprised six tree species and 37 animal species (40% exclusive species) (Appendix Fig. A.1). The network in GFB was composed of eight tree species and 50 animals in wet season (40% exclusive species) and nine fruiting tree species and 43 animals in dry season (33% exclusive species) (Appendix Fig. A.2). The 10 most common frugivore species (core group) shared five species between seasons in GFA (Appendix Fig. A.1) and six in GFB (Appendix Fig. A.2).

Connectance, specialization and links per species were different between seasons (CIs did not overlap) in GFA as expected by our hypothesis. However, no network parameter differed between seasons in GFB (Table 1).

All patterns from wet and dry seasons in GFA and GFB were significantly different from null models ($p < 0.05$), except nestedness for wet ($p = 0.11$) and modularity for dry ($p = 0.25$) in GFA, and nestedness for wet ($p = 0.39$) and modularity for wet ($p = 0.11$) and dry ($p = 0.32$) in GFB. Fruiting tree species strength differed between seasons in GFA (Dry-Wet, Estimate = -17.37 ; $t = -25.32$; $p < 0.01$; Residual deviance = 0.59733 on 92 degrees of freedom) and GFB (Dry-Wet, Estimate = 2.91; $t = 6.69$; $p < 0.01$; Residual deviance = 8.0724 on 201 degrees of freedom) showing increased interaction by trees in dry (GFA) and wet (GFB) seasons. Morphology (seed width) and nutritional content (lipid) of the diaspore were related with interactions of the frugivory networks (fruiting trees species strength) in different ways in each season (Table 2). Lipid-rich species with low variation in seed width were more common in GFA during dry season and in GFB during wet season (Appendix Table A2).

4. Discussion

Network parameters varied between seasons in GFA as initially hypothesized: more links between species in dry season and more specialized interactions during the wet season. Nevertheless, no one parameter varied between seasons in GFB, indicating that seasonal variation in networks is not necessarily consistent over time or space. Frugivores can use resources from a wide range of fruiting trees and fruiting trees can be visited by a diverse community of vertebrates (Hawes and Peres, 2014). As a consequence, low levels of specialization and high connectance are characteristics of some fruit–frugivore networks (Bascompte and Jordano, 2007), regardless of seasonality (Santos et al., 2014). However, despite of most of tree species had been visited by a diverse community of vertebrates, some birds in core group of both seasons in GFB consumed fruits from few (two or three) tree species (e.g. *Tersina viridis* (Illiger, 1811); *Phyllomyias fasciatus* (Thunberg, 1822)

Table 2

Significant explanatory variables and respective interactions to fruiting trees species strength in generalized linear models for each gallery forest (GFA; GFB) according different seasons (wet and dry, dry such as intercept).

	Source of variation	Estimate	T value
GFA	Wet, Lipid	3.18	26.53
	Wet, Seed width	36.82	23.18
	Wet, Lipid:Seed width	−6.04	−25.07
GFB	Wet, Lipid	−0.41	−5.59
	Wet, Seed width	−3.85	−6.93
	Wet, Lipid:Seed width	0.5	5.07

and *Turdus subalaris* (Seeböhm, 1887) in wet season; *Elaenia chiriquensis* Lawrence, 1865 and *Elaenia obscura* (d'Orbigny and Lafresnaye, 1837) in dry season), besides the birds that were outside the core group and consumed fruits from just one tree specie (Appendix Fig. A.2). In this way, these species can explain the similar and not so low specialization (H_2) values between GFB networks. The large number of frugivore species that was recorded in GFB can also explain the lack of seasonal differences in networks in that forest. Despite of more insectivores in core group of network dry season (four species, genus *Elaenia*) than wet season (two species, genus *Elaenia* and *Phyllomyias*) (Appendix Fig. A.2), in general there were many omnivorous birds in both seasons (28 species in each season, about 60% of the total, Appendix Table A.3). That guild of birds can interact with many fruiting trees and influence connectance and links per species (Baiser et al., 2012). Moreover, migratory birds can be abundant in Brazilian savannas between the end of dry season and the middle of wet season (Negret, 1988) and may, as a consequence, be able to influence connectance and other metrics in both seasons (Ramos-Robles et al., 2016). A bird with known migratory habit, *Elaenia chiriquensis* (Lawrence, 1865), was in core group of GFB wet and dry season (Appendix Fig. A.2) and *Turdus subalaris* (Seeböhm, 1887), other known migratory bird in Cerrado, is in core group of GFB wet season (Appendix Fig. A.2) and GFA dry season (Appendix Fig. A.1).

Some network parameters, however, did differ between seasons mainly in GFA. In Brazilian savannas, seasonality in availability of resources (higher in wet season) (Gouveia and Felfili, 1998) and in mutualistic interactions (Del-Claro and Oliveira, 2000) can affect fruit–frugivore interactions. Greater availability of fruits in one season may, for example, lead to increased richness and abundance of frugivores (Mulwa et al., 2013). Fruits can be an important available source of food in dry seasons and, therefore, may lead to an increase in connectance, links per species and generalization (low specialization). On the other hand, the presence of other food types, including fruits produced by shrubs or other, unsampled, trees or invertebrates, can also influence the interactions in networks (Gonzalez-Castro et al., 2012), decreasing connectance and links per species and increasing specialization, as was seen in the

Table 1

Networks parameters for each gallery forest (GFA; GFB) and season (W, Wet; D, Dry) with confidence interval by 95% quantiles obtained by randomization with replacement (1000 bootstrap samples). H_2 = specialization.

	Connectance	Links per species	H_2	Nestedness (NODF)	Modularity
GFA-W	0.24 (0.21–0.25)	1.21 (1.03–1.22)	0.73 (0.68–0.82)	18.61 (11.34–25.53)	0.45 (0.39–0.51)
GFA-D	0.28 (0.26–0.3)	1.46 (1.31–1.51)	0.55 (0.53–0.63)	23.73 (19–27.39)	0.34 (0.29–0.42)
GFB-W	0.28 (0.25–0.32)	1.96 (1.76–1.94)	0.51 (0.49–0.57)	31.03 (25.86–32.64)	0.261 (0.12–0.44)
GFB-D	0.28 (0.24–0.33)	2.08 (1.79–2.04)	0.44 (0.44–0.53)	30.57 (27.16–33.79)	0.2 (0.12–0.42)

GFA network during the wet season. Insectivorous animals were recorded less often in the wet season than in the dry season network in this forest (Appendix Table A.3), most likely because of the greater availability of insect prey in the wet season. In Brazilian savannas, three insect orders were most abundant during the wet season (Pinheiro et al., 2002) and all orders that were sampled, except Diptera, were more abundant at the beginning of the rainy season (Silva et al., 2011). Thus, some insectivores can eat fruits instead of insects in dry season, if fruits are easier to catch than insects, according to optimal foraging theory (Hughes, 1993). Moreover, diaspore characteristics (e.g. small size) (Howe, 2016) and high abundance of fruits and fruit-eating animals (Plein et al., 2013; Hawes and Peres, 2014), in addition to a long fruiting season (Gonzalez-Castro et al., 2012), can increase the interactions and, thus, help explain the differences between seasons.

Variation in the structure of ecological networks may be also influenced by urbanization and other anthropogenic disturbances (Sebastián-González et al., 2014) that can decrease the richness of frugivores (Gonzalez-Castro et al., 2012) and seed removal rates (Boissier et al., 2014). Frugivory networks in perturbed forests can therefore be less stable over time (Dupont et al., 2009). Most frugivores recorded in GFA were small species (Appendix Table A.3) that can consume usually small fruits given the limitation of gape size (Galetti et al., 2013). Thus, large frugivores can exert a greater influence on network parameters such as links per species (more) and specialization (less). In GFB, seven large frugivores were recorded – six birds and one monkey (Appendix Table A.3) – with substantial contributions to networks mainly in dry season (e.g. *C. cristatellus*, among the 10 most common frugivores). The data used to construct GFB networks were collected between 1988 and 1990; at that time the human environmental impacts in this region might have been lower (Klink and Machado, 2005). Moreover, other forests linked or close to GFB may have had a positive influence on overall species richness because of the relation between frugivore richness and large protected areas (Galetti et al., 2013). On the other hand, the difference in the frugivore community between two forests also may be affected by local environmental conditions which cause variation in fruit ripening times and fruit availability (Moran and Catterall, 2014). Frugivore frequency was higher in both seasons in GFB than in GFA (amount of frugivores in networks) and there were few hours of observation without any records of fruit-eating by animals in that forest.

Species composition and abundance of frugivores varied between seasons in both forests. These changes in the frugivore community may represent new trophic strategies and thereby lead to changes in networks parameters, as seen in GFA (Baiser et al., 2012). In GFB, however, the large number of animal species that interact with plants can mean greater overlap among animals (e.g. omnivorous birds) in ecological functionality (e.g. frugivory). This greater overlap means that the networks may be insensitive to some changes in abiotic factors and, consequently, may remain stable over time (Dupont et al., 2009).

Furthermore, nestedness, although common in tropical plant-animal networks (Sebastián-González et al., 2014), was not significant in the wet season in either forest. The presence of interactions between specialists may be responsible for this result. Specialist frugivores consume a fixed and small subset of fruiting species (Gonzalez-Castro et al., 2012). Also, restricted interactions with few plant species can change some generalist animals into specialists (Armbruster, 2006) (e.g. *Tangara cayana* and *Protium spruceanum*; *Turdus leucomelas* and *Euterpe edulis* in GFA wet season, Appendix Fig. A.1). Thus, the number of fruiting trees in the gallery forests probably was not enough to define a core interaction group and, hence, to result in significant nestedness in the network. Species that usually consume fruits (e.g. some Thraupidae and Turdidae

species) may also be responsible for the significant modularity seen in the wet-season network in GFA. Modularity is typically low in tropical ecosystems because of increased interactions with generalist frugivores (Schleuning et al., 2014). Thus, the absence of significant modularity in GFB indicates more generalized interactions, or that all fruits are being eaten by a wide range of frugivores, a condition which may be common to fruit-frugivore interactions (Howe, 2016) regardless of season. In this way, nestedness and modularity may not be related to precipitation seasonality (Sebastián-González et al., 2014), as in the networks from both forests analyzed in this study.

The species strength for fruiting trees varied over time and responded differently between seasons according to the lipid content and seed width of fruits found in gallery forests included in this study, as expected from the initial hypothesis (i.e., there will be the relationship between diaspore traits and plant-frugivores interaction in each season). In seasons where the presence of fruits with high lipid content was low, this nutrient was significantly related to greater increase of species strength regardless of the gallery forest in question. In GFA and in GFB, there was a greater presence of small diaspores with high lipid content in the dry and wet seasons, respectively, which can explain the positive relation between the interaction of lipid content and seed width with fruiting trees species strength. Network microscopic metrics (i.e., measures related with properties at a species level) can reveal strong fluctuations at the finer level because species features that vary in time and space (Trøjelsgaard and Olesen, 2016). The fruiting process in different seasons can be affected by different biotic and physical factors that can influence fruit characteristics (Piper, 1986) and, hence, the interactions with frugivores (Hawes and Peres, 2014).

Seed width was an important influence on tree species strength in seasonal networks where the range of this measure was higher. However, that range may not have been enough to limit interactions with frugivores (Galetti et al., 2013). It can be associated with variation in fruit size (correlation between seed size and fruit size, $r^2 > 0.6$; $p < 0.01$) which may represent an increase in available resources and attract, in this way, more consumers (Piper, 1986). Small diaspores with high lipid content are associated with frugivores birds and increased seed dispersal chances (Jordano, 1995). Birds were the most common frugivores in our networks and they may choose lipid-rich fruits rather than those rich in other nutrients, since lipids are negatively correlated with fruit carbohydrate content (Schaefer et al., 2014). Lipids may be more important in specific seasons such as before or during migration (Loiselle and Blake, 1991). The consumption of specific fruits to supply seasonal nutritive needs is common in birds (Gonzalez-Castro et al., 2012). Moreover, some species always look for lipid-rich fruits, accumulating this nutrient throughout the year (Loiselle and Blake, 1991). Nevertheless, lipids also may not vary seasonally (Piper, 1986) and were not related with frugivore choice (Piper, 1986; Muñoz et al., 2017). Sometimes, random choices (Poston and Middendorf, 1988) or more available fruits (Muñoz et al., 2017) are behind fruit consumption. Plant species with smaller seeds are important to network structure (Vidal et al., 2014) because they attract a generalist set of frugivore species (Hawes and Peres, 2014) that remove a large amount of fruits (Muñoz et al., 2017). Furthermore, the diaspore size is also important to define specialized interactions because birds and mammals differed significantly in their preference for fruit size (David et al., 2015).

4.1. Conclusions

Though we are cautious about extrapolating our results beyond gallery forest, our results suggest that despite very strong

seasonality, tropical frugivory networks may not necessarily vary seasonally. However, some changes in level of interaction species (microstructure of networks) can be possible. Future studies testing for seasonal variation in structure should survey multiple sites simultaneously to control for annual variation in fruit production. Moreover, studies testing phylogenetic signal among fruiting trees and frugivores that consume their fruits are also suggested, since it may influence some network parameters (Rezende et al., 2007) irrespective of seasonality. Finally our results emphasize that when using the results of network analyses to draw conclusions for conservation and management, the local diversity of frugivores and resource availability may have much greater effects than those of seasonality on community-wide trends in these key plant-animal interactions.

Author contributions

AABD, CBRM and JCM-J originally formulated the idea, AABD and JCM-J conducted fieldwork, AABD, JCM-J and CSF generated lipid analyses, AABD and EMB conceived this study, AABD and EMB performed statistical analyses, AABD, JGB and CBRM wrote the manuscript, EMB and JGB provided editorial advice, CBRM supervised the study.

Conflict of interest

AABD received Sandwich PhD grants from Coordenação de Aperfeiçoamento de Pessoal de Nível Superior. The authors declare that they have no conflict of interest.

Ethical approval

This article does not contain any studies with human participants or animals performed by any of the authors.

Acknowledgements

We are grateful to the Instituto do Meio Ambiente e dos Recursos Hídricos do Distrito Federal – Brasília Ambiental for permission to work in ESEC-AE gallery forest. We also thank Mauro Galetti and Marco Aurelio Pizo for helpful comments and suggestions.

Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.actao.2017.08.003>.

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